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THE NON-MUSCULAR ARTICULATIONS OF CRINOIDS

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IT has been long known that the non-muscular articulations in the crinoid arm, synarthries or bifascial articulations, and syzygies, have an entirely different effect upon the arm structure than do articulations possessing muscle bundles, straight or oblique muscular articulations. The muscular articulations are composed of three elements (Figs. 1 and 7); (1) the dorsal ligament, bounded ventrally by a strong transverse ridge running across the middle of the joint face, (2) the interarticular ligaments, just ventral to the transverse ridge, occupying triangular areas one on each side of the central canal, and (3) the muscle bundles, occupying two large distally rounded areas, separated by a narrow median ridge or furrow; in straight muscular articulations (Fig. 1) the transverse ridge separating the dorsal ligament fossa from the interarticular ligament fossæ runs at right angles to the dorsoventral axis of the joint face, and the two interarticular ligament fossæ and two muscular fossæ are of equal size, while in oblique muscular articulations (Fig. 7) the transverse ridge is strongly diagonal in position, and the two interarticular ligaments and two muscular fossæ are, on one side crowded, on the other drawn out, and therefore unequal.

The non-muscular articulations (Figs. 5 and 11) are

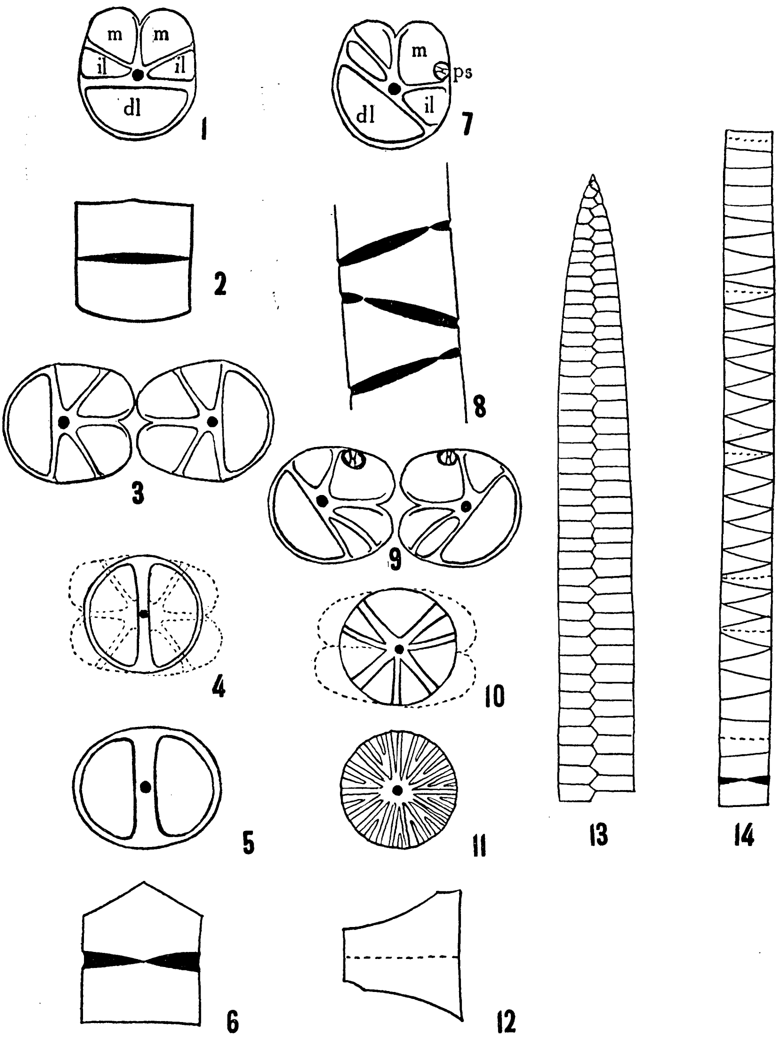

FIG. 1. Articular Face of a Straight Muscular Articulation; *m*, muscular fossæ; *il*, interarticular ligament fossæ; *dl*, dorsal ligament fossæ.

FIG. 2. Dorsal External View of a Straight Muscular Articulation between two Ossiclés-

FIG. 3. Two straight Muscular Articulations revolved through an Angle of 90°.

FIG. 4. The same, superposed so that their central Canals Coincide.

FIG. 5. A synarthry.

FIG. 6. External Dorsal View of a Synarthry between two ossicles.

FIG. 7. Articular Face of an Oblique Muscular Articulation; *m*, muscular fossa; *ps*, pinnule socket; *il*, interarticular ligament fossa; *dl*, dorsal ligament fossa.

bound together with ligament fibers similar to those of the dorsal ligament of muscular articulations; in synarthries (Fig. 5) these fibers are segregated into two large bundles lateral in position, separated by a dorso-ventral ridge across the joint face; in syzygies (Fig. 11) the fibers are scattered over the whole joint surface, which is broken up into alternating ridges and furrows radiating outward from the central canal, which may, in certain of the more specialized forms, such as the Pentacrinitidæ, become obsolete except about the periphery of the joint face.

Muscular articulations are often doubled, thus forming an axillary from which two arms arise; this never happens in the case of non-muscular articulations; moreover, muscular articulations are primarily pinnulate, the pinnule arising from a pinnule socket in the proximal outer part of one of the muscular fossæ. The difference between straight and oblique muscular articulations was originally a difference in pinnulation. In the most primitive type of crinoid arm found among the recent forms, occurring in the family Pentametrocrinidæ, we find the following sequence of articulations: (1) straight muscular, uniting the radial to the first post-radial joint, (2) synarthry, uniting the first two post-radial joints, (3) oblique muscular, uniting the second and third post-radial joints; all the succeeding articulations are oblique muscular, except for the interpolation of occasional syzygies. The first oblique muscular articulation bears the first pinnule; the addition of a pinnule socket on one side of the joint face causes a certain amount of crowding, and a conse-

FIG. 8. External Dorsal View of three oblique Muscular Articulations.

FIG. 9. Two Oblique Muscular Articulations revolved through an angle of 90°.

FIG. 10. The same, superposed so that their central Canals Coincide.

FIG. 11. A Syzygy.

FIG. 12. External Dorsal View of a Syzygy between two Ossicles; note how its course across the arm is the mean of the course of the preceding and succeeding oblique muscular articulations.

FIG. 13. A Biserial Crinoid Arm.

FIG. 14. A Monoserial Crinoid Arm, showing the triangular joints, the indices of an ancestral biserial arrangement.

quent depression dorsally of that half of the transverse ridge, which is compensated by a ventral depression of the opposite half; this alteration in one half of the transverse ridge is a necessary consequent of any alteration in direction of the other half, for the transverse ridge is the fulcrum upon which the bending of the arm occurs, and the fulcrum must always be a straight line to admit of any motion at all. Although primarily pinnulate, in certain rare cases oblique muscular articulations are sometimes found non-pinnulate, as in *Atelecrinus, Hypalometra, Cyllometra,* and *Perometra;* but this is a purely secondary condition, and one peculiarly prone to reversion, showing it to be somewhat unstable. In all cases, the position of the first oblique muscular articulation is the second articulation beyond the last straight muscular articulation of the arm. The oblique muscular articulations always alternate in the position of their diagonal transverse ridges, and the transverse ridges of succeeding joints form angles of approximately 90° with each other; therefore, a single brachial has proximally an articular face with the transverse ridge from a left ventro-lateral to a right dorso-lateral point, and distally an articular face with the transverse ridge running from a left dorso-lateral to a right ventro-lateral position. The pinnule socket always occurs on the side on which the end of the transverse ridge is dorso-lateral in position; hence, pinnules occur on alternate sides of the arm at succeeding articulations. In reality, of course, the alternation of the pinnules is the fundamental cause of the alternation in the direction of the transverse ridge, but, from the absence of pinnules on oblique muscular articulations in certain recent types, it is more convenient to speak of it as if the reverse were the case.

Non-muscular articulations are never doubled, are never pinnulate, and moreover, never affect the pinnulation in any way; the pinnule on the next succeeding muscular articulation is on the opposite side from that of the preceding muscular articulation, just as if the non-mus-

cular articulation were not there, but the two joints connected by it merely a single joint.

Of the non-muscular articulations, the synarthry occurs in the proximal part of the arm, the last synarthry immediately preceding the first oblique muscular, and immediately succeeding the last straight muscular articulation; all the non-muscular articulations succeeding the first oblique muscular articulation are always syzygies. In the simple arms of the Pentametrocrinidæ we find a straight muscular articulation, a synarthry, and then a series of oblique muscular articulations, interspersed with occasional syzygies. In this family the first brachial immediately follows the radial; but in all the other comatulids and in the recent species of the Pentacrinitidæ (except in the genus *Metacrinus*) the first brachial is separated from the radial by one or more interpolated division series, each composed of a reduplication of the first two brachials interpolated between the primitive first brachial and the radial. In these, however, the structure is the same; a series of synarthries alternating with straight muscular articulations occurs up to the first oblique muscular articulation, beyond which are found only oblique muscular articulations and syzygies. This is the primitive arrangement of the comatulid and pentacrinite arm, no matter how many times division may occur; but in certain specialized types, as *Endoxocrinus* and the Zygometridæ, one or more of the synarthries may be secondarily replaced by syzygies.

From the above discussion it is evident that (1) non-muscular articulations are morphologically radically different from muscular articulations; and (2) that there is a distinct interrelation between the two types of muscular articulations and the two types of non-muscular articulations; that is, that proximal to the first oblique muscular articulation *only straight muscular articulations and synarthries are found,* while distal to the first oblique muscular articulation occur *only oblique muscular*

articulations and syzygies; moreover, the synarthries always alternate with the straight muscular articulations, while the occurrence of the syzygies is more or less, and often very, irregular.

Bearing these facts in mind, we are able to reach a definite concept of the morphological significance of the synarthries and syzygies, in terms of straight and oblique muscular articulations. We have seen that the transverse ridges of succeeding oblique muscular articulations are always approximately at right angles to each other, and we may from this infer a fundamentally alternate position in all muscular articulations. The first articulation, uniting the radial to the first post-radial joint is straight muscular, with the transverse ridge at right angles to the dorso-ventral axis of the joint faces; according to what we found to be the case in oblique muscular articulations, the next articulation should be straight muscular, with the transverse ridge at right angles to that of the first, or coinciding with the dorso-ventral axis; but such an arrangement would leave the muscles and the interarticular ligaments on one side of the arm, and the dorsal ligament on the other, which would be manifestly absurd; but we actually find a transverse ridge running along the dorso-ventral axis of the joint face, with on either side of it a dorsal ligament bundle, *in every way the same as the dorsal ligament bundle of the preceding straight muscular articulation.* The synarthry, then, appears to consist fundamentally of the dorsal ligaments of *two* straight muscular articulations, abutting upon a common transverse ridge, which is at right angles to the transverse ridge of the preceding straight muscular articulation (Figs. 3 and 4). Not only does the microscopical comparison of the two individual muscle bundles of the synarthry with the dorsal ligament bundle of the straight muscular articulation bear out this interpretation of the origin of the synarthry, but the morphological effect of the synarthy upon the arm structure is at once explained. Non-muscular articulations never bear pin-

nules; pinnules are borne upon the muscular fossæ of muscular articulations; in the projection of one straight muscular articulation upon another to form the synarthry, the interarticular ligaments and the muscles are cut out, and only the dorsal ligament remains; with the elimination of the muscular fossæ, the pinnule sockets are lost; hence, synarthries can never bear pinnules, as the pinnule-bearing element of the articular face is omitted from their composition. Synarthries never affect the pinnulation; if a pinnule be borne on the left side of a straight muscular articulation preceding a synarthry, the pinnule on the next succeeding straight muscular articulation will invariably be upon the right side. A synarthry is primarily composed of two coalesced succeeding muscular articulations, one of which potentially bears a pinnule upon the opposite side from that of the other; these two primitive elements of the synarthry, being of exactly opposite tendencies in respect to their pinnules, counteract each other upon being merged, and hence we find the synarthry neutral in regard to pinnule arrangement; the synarthry possessing primarily (morphologically) *two* pinnules, the next following muscular articulation has its pinnule thrown to the opposite side of the arm from that on the muscular articulation preceding. Thus a synarthry, in reality, instead of having no effect upon the pinnule arrangement, has a double effect (though with the same result), throwing the pinnule to one side of the arm and back again within the compass of a single articulation.

Muscular articulations are frequently doubled, thus forming an axillary from which two similar arms arise; synarthries are never doubled; they are already double articulations, and a further doubling would be equivalent to a quadrupling of muscular articulations.

The syzygy is different from the synarthry only because it is formed from two *oblique* instead of *straight* muscular articulations (Figs. 9 and 10). A rotation of a straight muscular articulation through 90° brings the

transverse ridge into the dorso-ventral axis; hence, the transverse ridges of the two primitive straight muscular articulations coincide, and remain unchanged in the resultant synarthry; a rotation of two succeeding oblique muscular articulations 90° will, as their transverse ridges are already at right angles to each other, keep them in the same relative position; projecting one of them upon the other, the two transverse ridges form a right-angled cross; since the muscles and interarticular ligaments, being recessive when compared with the dominant dorsal ligament, disappear, we get an articulation consisting of a mass of dorsal ligament fiber crossed by radiating ridges. This crossing of the two fulcra upon a single joint face effectually prevents any movement at the articulation, and thus we get the primitive syzygy. The multiplication of the radiating ridges is without doubt a secondary development, though possibly four of them represent the distal edges of the interarticular ligament fossæ. The interpretation of a syzygy as a combination of the ligaments of two oblique muscular articulations explains the uniformly single condition of the syzygy, the absence of pinnules, and the neutrality of the syzygy in regard to pinnulation, this being brought about in the same way as in the synarthry, the resultant of two straight muscular articulations.

The interpretation of synarthries and syzygies just proposed involves a doubling up and merging together of the elements of two muscular articulations. This, it might well be argued, would be an occurrence improbable in the extreme in a linear series of joints and articulations. The ambulacral system of echinoderms, however, is composed primarily of a double series of joints, plates or whatever the elements may be, the first element alone being single. Thus in the urchins the oculars stand at the head of the double row of plates composing the ambulacra; and in the crinoids the radials stand at the end of an ambulacral system composed, in many genera, of two rows of plates, side by side, in biserial arrange-

ment. The similarity is even more striking; in the urchins new plates are added only between the ocular and the next succeeding plate, and it has been urged that the addition of new plates only at the ends of the arms in crinoids constitutes an important morphological difference between the ambulacral systems of the two groups. I have recently shown, however, that in almost all the recent crinoids (and similarly in many of the fossils) plates are added between the radials and next following joints (interpolated division series) just as in the urchins; the process of interpolation is different, but the result is morphologically identical in the two cases. J. S. Miller in 1821 first called attention to the similarity of a crinoid to an inverted *Cidaris*, but I believe the resemblance between the ambulacral systems of the two are closer and more fundamental than was supposed either by Lovén or by Carpenter. All the recent and most of the fossil crinoids have uniserial arms, but the brachials are always, at least in the proximal third of the arm, triangular or obliquely wedge shaped, a condition which is most pronounced in the young. Now, applying Jackson's law of "localized stages," we may assume in the crinoid arm that the joints which are ontogenetically the oldest are phylogenetically the oldest also; and we should thus be led to look for ancestral characters toward the arm bases. Here we find joints much more triangular than farther out, the distal and proximal ends being very oblique; hence we should infer an ancestry of forms with sharply triangular brachials; but certain comatulids go even farther in the proximal third of the arm, the brachials having borders so oblique that the inner apices of the triangles do not reach to the opposite border of the arm. Judging from recent forms alone, then (to say nothing of the fossils), we are irresistibly led to the conclusion that the biserial condition is the fundamental condition of the crinoid arm, just as the double row of ambulacral plates is the fundamental condition in the urchins, and that the monoserial arrangement is purely secondary,

an adaptation to special conditions of existence. The change from a biserial to a monoserial arrangement in the crinoids is merely a matter of an elongation of the arm, and a slipping in of the joints in one series between those of the other (Fig. 9). It has been suggested that *Encrinus, Platycrinus* and the other biserial crinoid genera are derived from monoserial ancestors because the new joints as they are formed at the arm tip are always monoserial in arrangement; but apart from the mechanical difficulties in the way of biserial termination to a free arm like that of the crinoids, we find that almost the same is true in the urchins; plates are added one by one abutting upon the median ambulacral line just behind the oculars, which move out by lateral growth first to one side then to the other, just as the monoserial plates at the tip of a *Platycrinus* or *Encrinus* arm, on increasing in size, more laterally first to one series, then to the other; the supposedly monoserial tip in biserial crinoid genera, therefore, appears to be, in reality not monoserial at all, any more than the proximal (post ocular) portion of the ambulacra in the urchins is monoserial.

The slipping in of the two series of joints in the biserial crinoid arm in the transition from a biserial to a monoserial condition undoubtedly first gave rise to synarthries and syzygies, the former originating from the coalescence of two straight muscular articulations, the latter from the coalescence of two oblique muscular articulations. I have been unable to study the joint faces of crinoids of the biserial type, and therefore have not traced the process, but, judging from the data at hand there seems to be much in favor of such an origin for spnarthries and for syzygies, and I hope to be able to adduce additional evidence in support of it in the future. A study of the ontogeny of *Antedon* does not help us, for in that type the synarthry and the syzygy are ontogenetically older than the beginnings of the deposition of calcareous matter, and the synarthry between the first two postradial joints is ontologically nearly or quite as

old as the phylogenetically much more primitive straight muscular articulation between the radial and the first postradial joint, and ontologically older than the straight muscular articulation succeeding it. Neither can we hope for any light when we know the embryology of the Pentacrinitidæ, for the early stages of the Pentacrinitidæ are undoubtedly practically the same as those of the comatulids, the only tangible difference in the adults being an enormous increase in the number of the short discoidal joints occurring at the top of the *Antedon* stem, and (of secondary importance) the retention of the stem. I have only been able to examine a very few fossils in regard to the interbrachial articulations; the results of my study of *Vintacrinus* have already been published; *Pentacrinites* (''*Extracrinus*'') is exactly like *Isocrinus* (restricted, *i. e.,* excluding *Endoxocrinus*) except for the small detail of the heterotomous instead of dichotomous condition of the extraneous division series, and *Marsupites* is exactly like *Antedon,* even in the position of the proximal syzygies; but I am convinced that a detailed and careful study of the articulations and articular faces of the joints in the fossil crinoids is one of the best lines of procedure in the elucidation of their systematic relations.